THE GROWTH OF LEAVES

THE University of Nottingham held its third Easter school in agricultural science during April 23–25. It took the form of a discussion, with demonstrations, on leaf growth. Prof. F. G. Gregory (Imperial College, London) opened the symposium by outlining some general aspects of leaf growth. The initiation of leaf primordia poses certain questions, especially if a hormone theory is invoked, since two groups of cells arise from the same apex—one forms a leaf capable of only limited growth and the other the axillary bud with the potential of unlimited growth. Cessation of cell division restricts the growth of the leaf, the size of which is determined by the number of primordial cells, the rate and duration of division and the size of the mature cells. Analysis of the growth curves of leaves can assist in understanding the way in which various factors influence leaf development. Temperatures below the optimum, for example, mainly influence the rate of growth of the primordia. A photochemical reaction is involved in the production of specific leaf-forming substances; but the nature of the reactions involved in leaf growth is little understood. Prof. E. Bünning (University of Tübingen) pointed out that capacity for division and unlimited growth are common properties of protoplasm, but that these are restrained by polarity and the close proximity of meristematic areas. Meristemoids arise in areas sufficiently removed from other meristems, and these in turn tend to suppress this tendency to unlimited growth. The self-duplication of substances produced by developing cells is responsible for the stable organization and ordered differentiation of the plant. The changes which occur during the growth and differentiation of cells were described by Drs. J. K. Heyes and R. Brown (Agricultural Research Council Unit of Plant Cell Physiology, University of Oxford). Cell enlargement is not simply the expansion of a metabolic system of constant pattern but involves a system in which the pattern itself changes. Metabolic activity is low in meristematic cells due to a high proportion of protein with low catalytic activity. During expansion, the relative proportion of catalytically active protein as well as the total protein increases, and there are changes in the activity of different enzymes which determine the rate and course of growth.

The inception of leaf primordia in several different plants was described by Prof. C. W. Wardlaw (University of Manchester). The position of inception of the primordium and its symmetry, orientation and rate of growth are regulated by the activity of the apex as a whole and can be disturbed by surgical and chemical treatments. There is need for much closer study of the constitution and metabolism of cells in the different regions of the apex, since these determine the formation of growth centres and control the geometrical pattern of leaf arrangement. This arrangement, or phyllotaxis, was rigidly defined by Dr. F. J. Richards (Imperial College, London), who indicated alternative methods of estimating phyllotaxis height. An equation was also derived which has wide applications to growing and dividing systems generally. In one form it yields a relation between the cross-sectional area of an apex, the slope of the apical surface relative to the longitudinal axis, the primordial insertion area, the plastochrone, and the difference between two transverse growth-rates; it then consists of two parts, each of which represents the phyllotaxis height corresponding to the particular plastochrone considered. The metabolic changes in such a system were examined by Drs. N. Sunderland, J. K. Heyes and R. Brown (Agricultural Research Council Unit of Plant Cell Physiology, University of Oxford). Such changes may be regarded as a consequence of the primary differentiation from the apex of the tunica with low metabolic activity and the corpus with high activity. Cell division and protein accumulation are restricted in the corpus; but substrates are transferred from it to the tunica to supply materials for the rapid division and protein synthesis which occurs in this region of low inherent synthetic activity. A similar pattern occurs during development of the leaf primordium when metabolic activity increases from a low to a high level.

The changes which occur at different stages during expansion, producing a variety of different leaf forms, were outlined by Dr. H. Jones (University College, Aberystwyth). In juvenile leaves the primordial form persists to maturity; in other leaves, changes may occur at an early stage of development and may also be related to changes in width of the shoot apex. Changes in shape during expansion result from localized differences in divisions and growth; these may be analysed by using the allometric relation. Size and shape may be altered by various physical and chemical agents. From defoliation experiments with apple, Mr. H. W. B. Barlow and Mr. C. R. Hancock (East Malling Research Station) postulated that at least three different substances or groups of substances are produced by leaves and influence the growth of other leaves. One of these groups probably consists of the major photosynthetic products, a second is a factor (or factors) produced by immature leaves which influences internode extension, and the third a leaf-growth factor which influences cell division. The influence of length of day on leaf development was discussed by Prof. E. Bünning (University of Tübingen). Short days accelerate leaf production by long-day plants and retard it in short-day plants, but the rate of ageing of leaves of both types is hastened in long days. Although there is little difference in the total growth made during the light and the dark period, there are definite fluctuations in growth-rate during these periods, the maximum occurring at different times depending on the species. Prof. W. T. Williams (University of Southampton) discussed the association of light with leaf growth in terms of the etiolation phenomena of leaf suppression and internode extension which is exhibited in its absence. Suppression of etiolation by brief flashes of light is associated with the initiation of cell division; but the amount of division set in train is out of all proportion to the light stimulus given. It appears that the synthesis of leaf proteins is automatically initiated by a brief period of light; the process once started continues, irrespective of further light.

During the final session, the effect of external factors on leaf growth was discussed. Prof. F. L. Milthorpe (University of Nottingham) emphasized that most changes occur during the primordial stage. Although low temperature retards all processes, differentiation of primordia appears to continue at a higher rate than does the rate of division and expansion of cells leading to growth of a leaf. The stage of growth is also important ; following a temperature check, a higher relative growth-rate of leaves occurs if some leaves have expanded than if no leaves are present. The influence of conditions at germination persists long into the growing period. Prof. G. E. Blackman (University of Oxford) discussed the effects of light and temperature on leaf growth. These vary with the species : reduction of light intensity below full spring and summer daylight may have little effect on the leaf area of one group of plants ; in another group, there may be a large increase in leaf surface with reduced light almost to the compensation point ; whereas in a third the effect may be intermediate. There is, in general, a direct curvilinear relation of net assimilation-rate and an inverse relation of the leaf area ratio with light intensity ; the resultant effect on relative growth-rate, being the product of these terms, depends on the magnitudes of the responses involved in these two relations. The retarding effect of increasing light on leaf expansion occurs with intensities greater than 300–600 ft.-candles ; at lower intensities there is a positive effect. Leaf area increases with temperature up to about 25° C., but interactions occur between different levels of temperature and light. Dr. H. L. Penman (Rothamsted Experimental Station) showed that the growth of grass is closely proportional to the total energy supplied at the surface, and also to the potential transpiration. Water becomes limiting at small values of soil moisture deficit ; these values are smaller with low than with high nitrogen supply. The slope of the curve relating growth to incoming radiation is also influenced by the nitrogen-level. Dr. D. J. Watson (Rothamsted Experimental Station) emphasized the general conclusion that the variation in dry-weight yield per acre is determined mainly by leaf growth. Variations in the rate of photosynthesis have little influence. The maintenance of dense leaf coverage during the major portion of the growth period provides the main possibility of increasing yield. There is a limit, however, to the increase in returns possible, as mutual shading of leaves ultimately reduces the net assimilation-rate sufficiently to offset the gain from the larger leaf surface. Yield of grain depends largely on a large leaf area during grain formation.

The points raised in the papers were vigorously discussed, and some of the conclusions and techniques used were demonstrated. Full proceedings will be published elsewhere. F. L. MILTHORPE

FRESHWATER BIOLOGY IN SCOTLAND

THE symposium during April 9–10 on freshwater biology in Scotland, arranged by the Institute of Biology (Scottish Branch), was the first occasion when a comprehensive survey of the progress of work on Scottish fresh waters has been presented. This being so, it is natural that it should cover a wide diversity of subjects. Subjects which ranged from the effects of hydroelectric schemes on migratory fish to the emergence of aquatic insects were submitted for discussion by speakers from the Universities of Edinburgh and Glasgow, the Brown Trout Research Laboratory, Pitlochry, the Oceanographic Laboratory, Leith, and the North of Scotland Hydro-electric Board. The topics brought forward for discussion in the first two sessions were not unrelated, and most can be fitted into a sequence commencing with conditions for life in Highland waters and passing to ecological aspects of the flora and fauna.

It was reported that streams of the catchment areas of Highland lakes and rivers are markedly subject to excessively rapid run-off, partly due to the removal of vegetation by clearing of timber and the burning of moors and partly also to extensive channel draining of sheep pastures. When peat is exposed it is not as efficient a water store as might be supposed. Rainfall reduces the surface layer to a colloidal gel, which inhibits deeper penetration and enhances rapid surface drainage into water-courses, which, in their upper reaches, usually flow down steep slopes. The result is extensive erosion in the lower reaches under storm conditions. Rapid drainage and influx of peat derivatives into Scottish lakes are contributory to the main cause, the mineralogical nature of the Highlands, of the paucity of plant nutrients in these waters. More than half those studied have a calcium content (expressed as $CaCO_3$) of less than 10 p.p.m. and nearly all have less than 50 p.p.m. They have not evolved to a degree of eutrophy permitting the reversible oxidation-reduction process described by Ohle[1] and Mortimer[2], with the result that plant nutrients tend to be occluded in the bottom muds and their main source lies in the small amounts brought in by inflowing streams.

Studies on phytoplankton in Scottish lakes, especially the application of Nygaard's[3] 'compound quotient' to a general survey, emphasize the oligotrophic nature of the majority. This quotient, which is the number of species characteristic of eutrophic waters (for example, species of Chlorococcales and Myxophyceae) divided by the number of species characteristic of oligotrophic waters (for example, species of Desmidaceae), displays a correlation with chemical evidence and with productivity of bottom fauna. Where past records exist, it has been possible to demonstrate the rate of evolution of a lake. Loch Leven, in Fife, with a quotient of 2, fifty years ago ranked as mesotrophic. To-day, with a quotient of 8, it is eutrophic. Loch Lomond, on the other hand, has shown no change over the same period.

Known in England only in the Lake District, the cladoceran crustacean, *Holopedium gibberum*, is absent from eutrophic waters but abundant in many oligotrophic lakes in Scotland. The conditions governing its distribution are not yet fully understood, for it is absent from some water bodies which appear to be closely similar to those in which it does occur. A possible clue to the uneven distribution is the presence of a certain minimum amount of dissolved organic material in the water.

The impermanence of fresh waters was discussed from another aspect, that of their invasion by pulmonate gastropods. It was suggested that the co-existence of pulmonates with a wide range of adaptations, from the great phenotypic plasticity and high ratio of selection—that is, number of individuals surviving to breed annually—of *Lymnaea peregra* to the great genotypic specialization and low ratio of selection of *Ancylus fluviatilis*, may be credited to the instability of freshwater habitats relative to their marine counterparts.

In papers on freshwater fishes and their parasites, during the second day of the meeting, interest lay in new or little-known occurrences in Scotland. Among